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1 Exceptionally high mangrove root production rates in the
2 Kelantan Delta, Malaysia; an experimental and comparative
3 study.

4 Siti Mariam Muhammad Nor^{1,6} Mark Huxham², Yann Salmon^{1,3} Symone Jade Duddy²,
5 Alban Mazars-Simon², Maurizio Mencuccini⁴, Patrick Meir^{1,5}, Gail Jackson¹.

6
7 ¹ School of Geosciences, Crew Building, The King's Building, University of Edinburgh,
8 EH9 3FF Scotland

9
10 ² School of Applied Sciences, Edinburgh Napier University EH11 4BN Scotland

11
12 ³ Faculty of Science, Department of Physics University of Helsinki 00014 Finland

13
14 ⁴ICREA at CREAF Universidad Autonoma de Barcelona Edificio C, 08290 Cerdanyola,
15 Barcelona Spain

16
17 ⁵ Research School of Biology, Australia National University, Canberra Australia.

18
19 ⁶ School of Marine and Environmental Sciences, Universiti Malaysia Terengganu, 21030
20 Kuala Nerus, Terengganu, Malaysia.

21
22 Corresponding author: G.Jackson@ed.ac.uk

23 Highlights

- 24 • A Malaysian mangrove forest shows exceptionally high annual root production
25 of 12.7 t ha⁻¹ yr⁻¹.
26
27 • Root productivity showed a strong seasonal trend, peaking during the monsoon
28 season.
29 • Root turn-over was exceptionally rapid (especially that of fine roots at 0.81 yr⁻¹).
30
31 • The root:shoot productivity ratio (at 2.65), was comparatively high.
32
33 • Fine root biomass was the major contributor to belowground biomass and
34 biomass production.

35
36

37

38 Abstract

39 Mangroves often allocate a relatively large proportion of their total biomass production
40 to their roots, and the belowground biomass of these forests contributes towards globally
41 significant carbon sinks. However, little information is available on root production in
42 mangroves due to the difficulties in carrying out measurements of belowground
43 processes, particularly if there is regular flooding. In this study, we examined fine and
44 coarse root production in the east coast of the Malaysian Peninsula. Ingrowth cores were
45 used over the course of 17 months. In September 2014, twenty cores were randomly
46 placed in each of five plots. Three cores were collected from each plot (fifteen cores in
47 total), once every three months. Each core was divided into five 10 cm layers and root
48 dry mass was recorded. Standing root biomass was also measured at the time of final
49 collection using an additional 15 cores. There was a seasonal pattern in root production,
50 which peaked in March and December 2015, after and during the monsoon season. Root
51 biomass in the cores peaked at $33.23 \pm 6.3 \text{ t ha}^{-1}$ and $21.46 \pm 7.3 \text{ t ha}^{-1}$ in March and
52 December respectively. Standing root biomass in February 2016 in the forest was 20.81
53 $\pm 2.8 \text{ t ha}^{-1}$. After 17 months, the final root biomass in the cores was 14% less than the
54 standing root biomass. These data suggest surprisingly rapid growth rates and turnover
55 for mangrove roots. Total root biomass significantly increased with root depth and 78%
56 of the roots, in all soil layers, consisted of fine roots ($< 3 \text{ mm}$ diameter). Soil carbon,
57 nitrogen and phosphorous concentrations were investigated in relation to belowground
58 production, as were soil temperature, salinity and dissolved oxygen. A data review of
59 global studies reporting similar work was carried out. The results are discussed with
60 consideration to the significance of monsoon rainfall for mangrove ecology.

61 Keywords: Root stock, root production, allocation aboveground, allocation belowground,
62 monsoon season, rapid root turnover.

63 Introduction

64

65 Mangrove forests are very productive ecosystems (Tomlinson 1986; Alongi 2012).
66 Carbon is fixed by the mangrove trees themselves and by associated algal communities
67 on the aboveground roots and forest floor (Alongi 2014). This autochthonous production
68 contributes to the large organic carbon reservoirs typically found in mangroves. In
69 addition, allochthonous inputs from adjacent freshwater and oceanic systems are trapped
70 and stored (Jannerjahn and Ittekkot 2002), with retention of this organic matter and
71 associated nutrients promoting the high primary productivity (Kumara et al. 2010). This
72 combination of high productivity, interception of allochthonous carbon and deep, anoxic
73 soils means mangroves can store exceptionally large amounts of carbon, particularly in
74 belowground deposits, and are one of the most carbon-dense ecosystems on Earth
75 (Donato et al. 2011; Gress et al. 2016).

76 Studies of mangrove productivity have focused mainly on aboveground biomass using
77 litter fall and stem diameter measurements (Gong and Ong 1990; Robertson and Alongi
78 1995; Sukarjo et al. 2013; Mitra et al. 2011). The litter fall data help to quantify total
79 productivity and illustrate the sources of organic matter available for secondary
80 consumption (e.g. by crabs), burial or export to the sea. Studies of stem diameter,
81 typically using allometric equations (e.g. Komiyama et al. 2005), provide information
82 concerning biomass accumulation in the tree trunk. However, recent years have seen a
83 growing interest in belowground biomass and productivity, given the roles of mangroves
84 as carbon sinks and coastal buffers. Most studies show mangrove ecosystems are efficient
85 carbon sinks, with the largest carbon stock (more than 90%) consisting of organic carbon
86 in the soil (Donato et al. 2011; Adame et al. 2015; Sanders et al. 2017). This finding is
87 consistent across mangrove forest settings such as estuarine and oceanic mangroves of

88 the Indo Pacific (Donato et al. 2011), different mangrove zonations (Kauffman et al.
89 2011), and natural or restored mangrove forests (Nam et al. 2016; Sahu et al. 2016).
90 Mangroves have specialized root systems, including aerial roots, which allow respiration
91 during submergence (Alongi, 2009). These complex aboveground features can reduce
92 water current velocity and encourage deposition of particles (Krauss et al. 2003; Kumara
93 et al. 2010). This process of accretion, and the expansion of roots belowground, can lead
94 to vertical elevation of the soil surface. For example, in Caribbean mangroves, refractory
95 roots and other organic materials (e.g. benthic mat algae, leaf litter, and woody debris)
96 are substantially responsible for soil formation (McKee et al. 2007). Surface elevation
97 driven by root growth and accretion can help ensure mangroves keep pace with rising sea
98 levels and help buffer coastlines against the effects of sea level rise (McKee 2011).
99 However, elevation can be inhibited or reversed by natural disturbances such as
100 hurricanes and storms which can cause soil elevation loss (Cahoon et al. 2003; Barr et al.
101 2012; Cahoon 2006). Similarly, human disturbances may contribute to rapid surface
102 elevation loss (Lang'at et al. 2014; Lovelock et al. 2015).

103 Understanding what controls mangrove root productivity, turnover and architecture is
104 therefore important in understanding the ecological functions of forests. Several studies
105 have explored the influences of environmental factors such as nutrients on biomass
106 allocation patterns in mangrove forests (e.g., Alongi, 2009). In depleted nutrient settings,
107 mangroves may allocate 40-60% of their production to belowground biomass (Komiyama
108 et al. 1987). This is a strategy for plants to manage their resources efficiently under
109 nutrient stress (Castaneda-Moya et al. 2011). In Floridian mangroves, soil phosphorus is
110 always limiting, which results in stunted forests. Riverine mangroves, growing in more
111 productive sites, tend to allocate proportionately more biomass to aboveground whilst
112 nutrient limited scrub communities show greatest biomass allocation belowground
113 (Castaneda-Moya et al. 2013). Mangroves in Micronesia also show greater proportional

114 root biomass associated with relatively low soil phosphorus (Cormier et al. 2000).
 115 Nutrient limitation can interact with other stresses however; for example in a karst lagoon
 116 in Mexico with high salinity, greater root biomass and production was found with higher
 117 soil phosphorus (Adame et al. 2014). Under long tidal submergence and limited nutrients,
 118 high root biomass but lower root production and root turnover were recorded (Castaneda-
 119 Moya et al. 2011), perhaps because tidal submergence limits root production.

120 Many other factors, in addition to nutrients, may influence root production, including
 121 tidal range, rainfall, salinity and soil temperature (Komiya et al. 1987; Saintilan 1997;
 122 Paungporn et al. 2016). Seasonality in mangrove root production has been observed, with
 123 the highest productivity recorded during the wet and early cool dry season (Paungporn *et*
 124 *al.* 2016). This suggests that root productivity is associated with increased rainfall and
 125 thus reduced salinity of porewater. Terrestrial forests show similar patterns, as seasonal
 126 root production in rubber trees correlates directly with rainfall (Maeght 2015).

127 Biomass allocation varies between mangrove species and tree stands. Fast growing
 128 species such as *Avicennia marina* allocate proportionally more biomass belowground
 129 under optimum environmental conditions, while *Rhizophora mucronata* invests more
 130 aboveground (Lang'at 2013). In Gazi Bay, Kenya, the highest belowground biomass was
 131 recorded in replanted mangrove forests rather than natural stands. *Sonneratia alba*
 132 showed the highest root biomass in comparison to *Avicennia marina* and *Rhizophora*
 133 *mucronata*, perhaps due to its exposed position at the seaward fringe, where investment
 134 in roots is needed to anchor the trees against wave impacts (Tamooch *et al.* 2008). There
 135 may also be complementarity between different root architectures; an experimental study
 136 at the same site demonstrated that mixed mangrove stands show greater proportional
 137 belowground productivity than monospecific ones (Lang'at *et al.* 2012).

138 Despite the newly discovered importance of belowground carbon storage in mangroves,
139 and hence the belowground processes that control it, we still know relatively little about
140 belowground productivity in mangrove forests and how it relates to aboveground
141 productivity. The current study examines belowground productivity in a Malaysian forest
142 and explores the influence of a range of environmental variables on root production. It
143 also investigates the relationship between above and belowground growth rates.

144

145 Materials and Methods

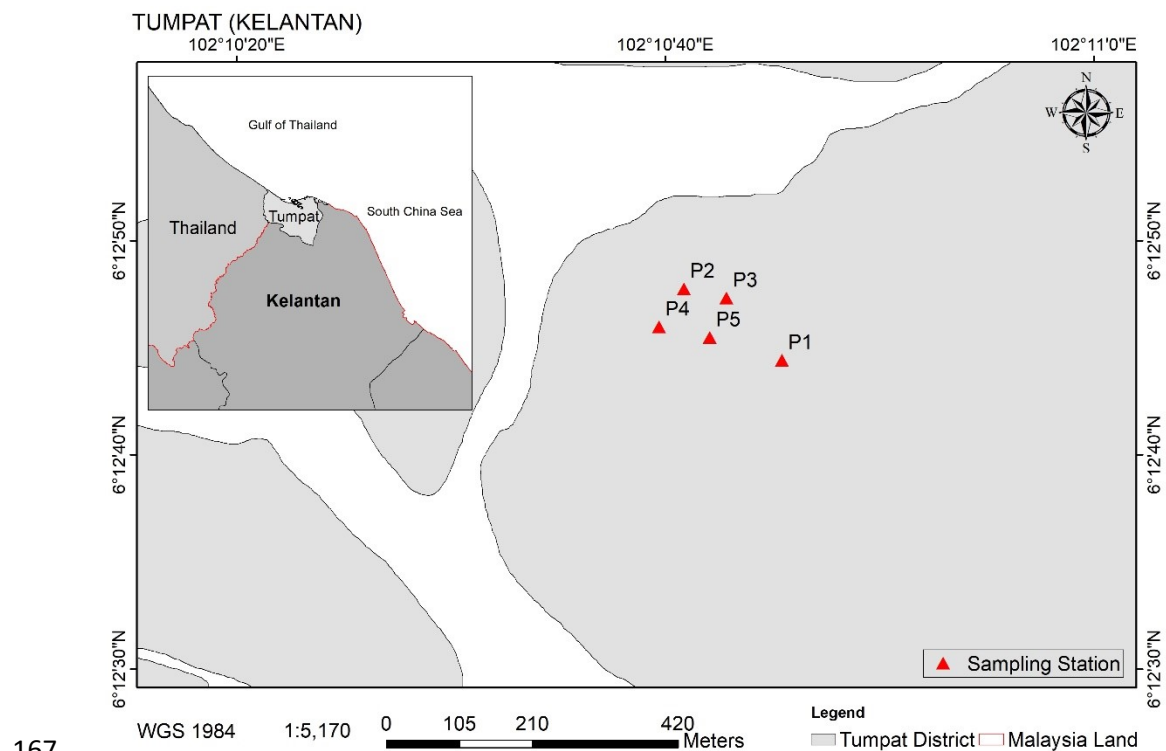
146 Study site

147 This study was conducted on the Kelantan Delta ($6^{\circ}12' 46.8''$ N $102^{\circ} 10'43.0''$ E), in the
148 state of Kelantan, on the east coast of the Malaysian Peninsula (Fig. 1). This area consists
149 of 17 small islands (Satyanarayana et al. 2010) with an estimated total deltaic area of
150 1200 ha (Shamsudin and Nasir 2005). This area experiences the monsoon from November
151 to March, which causes strong currents and brings flooding to adjacent settlements.

152 The annual rainfall in 2013, 2014 and 2015 was 2235 mm, 2999 mm and 2065 mm,
153 respectively (Malaysian Meteorological Department, 2016); with the highest and lowest
154 spring tides being 1.7 m and 1.4 m above chart datum (Malaysian Hydrographic National
155 Centre, 2018).

156 The Kelantan delta consists of distributaries channel fed by the Kelantan river flowing to
157 the South China Sea. It receives run-off due to seasonal rainfall and offshore currents,
158 which contribute to the coastal morphology and hydrographical condition (Mohd-Suffian
159 et al. 2004). The forest is composed of five dominant species: *Avicennia alba*, *Bruguiera*
160 *gymnorhiza*, *Nypa fruticans*, *Rhizophora mucronata* and *Sonneratia caseolaris*
161 (Satyanarayana et al. 2010). Based on species composition and stand structure, two main

162 vegetation groups are recognised in the delta. The first one, dominated by *S. caseolaris*
 163 and *N. fruticans*, is distributed throughout the forest, occupies low-lying to elevated
 164 ground and has low to medium salinity. The second group, largely dominated by *A. alba*,
 165 is present close to the bay-mangrove boundary, occurs at low to medium elevations and
 166 is characterised by relatively high salinity levels (Satyanarayana et al. 2010).



169 Figure 1. The location of the study site in the Kelantan Delta on the Malaysian Peninsula.

170 The locations of the five *Avicennia alba* study plots are shown by red triangles.

171

172 Sampling plots

173 The experiment was set up in a natural stand of *Avicennia alba*, representative of the
 174 corresponding vegetation group in the Kelantan Delta, in September 2014. Five plots of
 175 10 m x 10 m (0.05 ha in total) were established in the mangrove forest (Fig. 1). The plots

176 were chosen randomly to be representative of the area of *A. alba* in the stand. All plots
177 were inundated daily at high tide.

178 Above ground monitoring

179 In September 2014 all the *A. alba* trees in each plot were tagged and height and diameter
180 at breast height (DBH) recorded. The point at which DBH was measured was marked to
181 permit accurate repeat measurements at the end of the study in February 2016.

182 Aboveground biomass was estimated using DBH in the allometric equation developed by
183 Komiyama et al. (2005) for mangrove forests of Southeast Asia:

$$184 \text{ Aboveground biomass (kg ha}^{-1}\text{)} = 0.251 \times \rho \times \text{DBH}^{2.46}$$

185 Where ρ (wood density) = 0.560 kg m⁻³

186 Aboveground biomass was estimated at the beginning and end of the study (a period of
187 17 months) and scaled to produce an annual productivity value.

188

189 Ingrowth core installation

190 A total of 100 ingrowth cores (50 cm depth x 15 cm diameter) were placed between 1 and
191 2 m from major tree trunks, within the five plots, with twenty cores per plot. They were
192 made of plastic mesh (sub-mesh size 1 cm x 1 cm) and inserted vertically to 50 cm depth.

193 To install the cores, a 50 cm deep hole was dug and all the soil removed. All roots found
194 within the soil were removed and chopped into small pieces and then returned to the soil
195 within the core, which was then placed within the hole. This procedure was carried out to
196 ensure representative nutrient conditions in the ingrowth cores, since simply removing
197 roots would remove an important source of nutrients (McKee 2001), while leaving them
198 uncut would have made distinguishing new root growth difficult.

199

200 Ingrowth core collection

201 Three ingrowth cores per plot were collected every three months throughout the study
202 period, i.e. 15 cores in total were collected in December 2014, March 2015, June 2015,
203 September 2015, December 2015 and February 2016. The cores were brought to the
204 laboratory and divided into five layers; 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and 40-
205 50 cm. The roots were washed from each layer using mesh sieves to remove the attached
206 soil particles and debris. They were then rinsed several times until they were free from
207 other materials. Finally they were soaked in water and the living roots separated from
208 the dead roots by hand. The live roots were sorted into two size categories; fine roots (<
209 3 mm diameter) and coarse roots (> 3 mm diameter). Very few dead roots were found,
210 therefore these are not included in the analyses. All roots were oven dried for
211 approximately 24 hours at 80°C until constant weight.

212 In February 2016 the root standing stock was assessed by collecting three additional cores
213 from each of the five plots (15 cores in total). Cores were 40 cm deep and 4 cm in
214 diameter and were collected between 5 to 10 m from major tree trunks.

215

216

217 Environmental parameters

218 In February 2016 a range of environmental parameters were measured in order to examine
219 the association between belowground production and environmental conditions.

220

221 *i) Soil nutrient analysis*

222 One soil core (15 cm diameter x 50 cm height) was collected from each of the five plots.
223 Each core was separated into five layers (0-10 cm), (10-20 cm), (20-30 cm), (30-40 cm)
224 and (40-50 cm), and each section was analysed separately. The soil was oven dried to
225 constant mass at 80°C for 72 hours and brought back to Edinburgh University, United
226 Kingdom. Soil was analysed for total phosphorus, total carbon, total nitrogen and the
227 C:N ratio was calculated. 10 mg of soil from each layer was weighed for the C and N
228 analysis and the samples measured using an elemental analyser (NC 2500, CE
229 instruments Ltd United Kingdom). Pseudo-total P was determined using an Aqua Regia
230 digestion. 20 g of finely ground soil was dried overnight at 105°C. From this, a 5 g
231 subsample was taken and ashed at 430°C overnight. Then 0.5 g of ashed soil was
232 dissolved in a 5:1 (v/v) mixture of HCl and HNO₃ (respectively) whilst heated to 100°C
233 in a water bath. The sample was evaporated to dryness then re-dissolved with 1ml of 1:1
234 HCl and filtered through a Whatman 4 filter paper into a 50 ml volumetric flask, then
235 made up to 50 ml with deionised water. The concentration of P was then measured using
236 an Auto Analyzer Applications III (Bran & Luebbe, Germany) using the molybdenate
237 blue procedure outlined in Stewart (1974).

238

239

240 *ii) Soil physico-chemical analysis*

241 Pore-water samples were collected at four random locations within each plot during low
242 tide for the determination of salinity, dissolved oxygen and soil temperature. Salinity was
243 examined using a refractometer (Kern optics ORA 1SA, United Kingdom) whilst
244 dissolved oxygen and soil temperature were recorded using a portable multiprobe
245 Pro2030 (YSI Inc., Ohio USA). The multiprobe was inserted to a depth of 30 cm and
246 allowed to settle for two to three minutes prior to measurements.

247

248 In order to describe the relationship between above and belowground productivity,
249 several parameters were calculated as follows:

250 i) Aboveground standing stock and production

251 Stem DBH data was incorporated into the allometric equation described above, following
252 Komiyama et al. (2005), to derive initial (September 2014) aboveground biomass (dry
253 weight) in t ha^{-1} and final aboveground biomass in t ha^{-1} (February 2016). The difference
254 in biomass between these dates was used to calculate annual aboveground production (t
255 $\text{ha}^{-1}\text{year}^{-1}$).

256

257 ii) Belowground standing stock and production

258 Roots were weighed and the units converted to gm^{-2} to allow comparison with other
259 studies. The surface area of cores used to calculate root production, was 176.74 cm^2
260 whereas the surface area of the cores used to calculate standing stock was 12.56 cm^2 .
261 These values were scaled and converted to t ha^{-1} for standing stock and $\text{t ha}^{-1} \text{ year}^{-1}$ for
262 root production.

263 Annual root production was calculated by taking the mean of each of the 6 three-month
264 root biomass totals and converting them to annual production in $\text{t ha}^{-1} \text{ year}^{-1}$.

265

266 iii) Root:shoot ratio of aboveground and belowground standing stock and production

267 Root:shoot ratios were calculated in order to determine allocation to above and
268 belowground components for both standing stock and production.

269 iv) Root turnover

270 Root turnover was calculated following Gill and Jackson (2000), by dividing annual root
271 production by root standing stock.

$$\begin{aligned} 272 \text{ Root Turnover (yr}^{-1}\text{)} &= \frac{\text{Annual belowground production (t ha}^{-1}\text{ yr}^{-1}\text{)}}{273 \text{ Maximum belowground standing stock (t ha}^{-1}\text{)}} \\ 274 \end{aligned}$$

275 Studies from around the world reporting similar research to that described here were
276 analysed and are summarised in Tables 4, 5, 6 and Figure 5.

277 Statistical analysis

278 Differences of fine, coarse and total root biomass and soil depth among the months of
279 collection were performed using one-way ANOVAs. Differences in aboveground
280 biomass between months were determined by one-way ANOVA. Log or square root
281 transformations were applied to meet ANOVA requirements for non-normal data. *Post*
282 *hoc* Tukey tests were performed to find significant differences between month of
283 collection and soil depth. Pearson correlations were performed to find relationships
284 between root and aboveground biomass among environmental variables, including soil
285 nutrients (carbon, nitrogen, C:N ratio and total phosphorus), soil temperature, salinity and
286 dissolved oxygen. Statistical analysis was performed using Minitab 17 software.

287

288 Results

289 Forest structure

290 Forest characteristics are shown in Table 1. There were no significant differences in any
291 parameters between the plots, therefore data have been combined.

292 Table 1. *Avicennia alba* forest structure in the Kelantan Delta. Mean \pm SE.

Forest characteristics	September 2014	February 2016
Tree density (stems ha ⁻¹)	1200 ± 0.52	1200 ± 0.52
Average DBH (cm)	17.58 ± 1.04	17.82 ± 1.04
Height (m)	14.13 ± 0.62	-
Basal area (m ² ha ⁻¹)	210.96	213.84

293

294 Environmental parameters

295 Physico-chemical parameters of the mangrove forest did not vary across the plots ($p >$
 296 0.05) and data have therefore been combined (Table 2).

297 The total amount of phosphorus, carbon, nitrogen and the C:N ratio did not vary
 298 significantly with soil depth. However although there were no statistically significant
 299 differences, there was a tendency for the nitrogen and carbon content to increase with
 300 depth. Phosphorus content and the C:N ratio remained consistent with depth. There were
 301 no statistically significant correlations between above and below ground production and
 302 soil nutrients and physio-chemical parameters.

303

304 Table 2. Environmental variables. Data recorded in February 2016 (n = 5).

Environmental data	Mean ± SE
Pore-water salinity (ppt)	12.08 ± 0.88
Pore-water dissolved oxygen (mg/l)	4.45 ± 0.96
Pore-water soil temperature (°C)	27.94 ± 0.08
Total soil phosphorus (% of mass)	0.12 ± 0.01

Soil carbon (% of mass)	2.45 ± 0.18
Soil nitrogen (% of mass)	0.04 ± 0.01
Soil C:N (% of mass)	81.57 ± 9.53

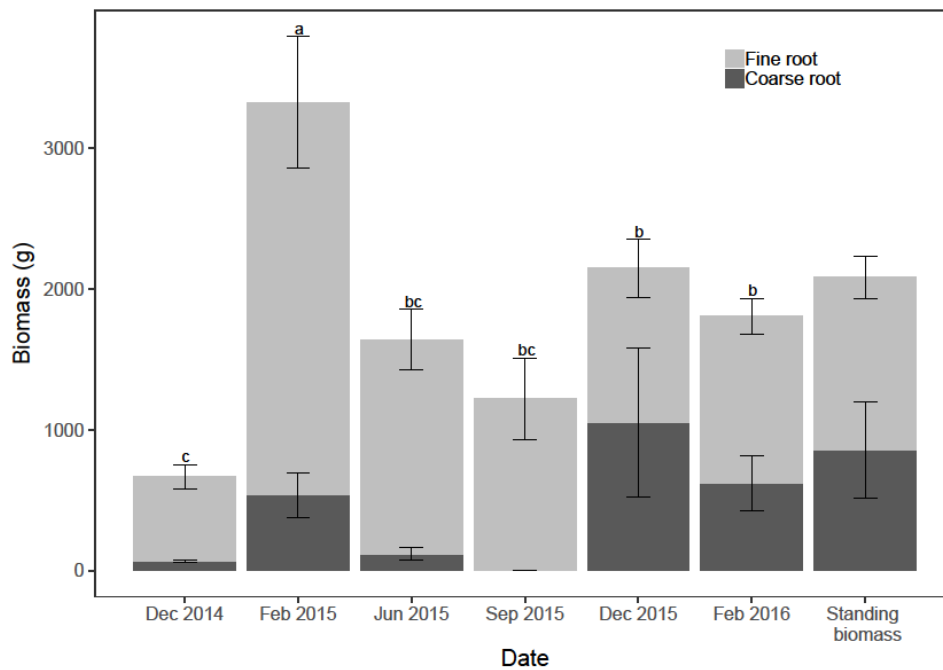
305

Belowground standing biomass and production

307 In February 2016, the mean root standing stock across all five plots was 20.81 t ha^{-1} (Table
308 3). The root biomass was $1225 \text{ gm}^{-2} \pm 123.8$ and $856 \text{ gm}^{-2} \pm 153.46$ for fine and coarse
309 roots respectively. 59 % of the total root biomass was therefore fine roots.

310 Total root production was significantly different across the months of collection ($p <$
311 0.001), ranging from $665 \pm 96.4 \text{ gm}^{-2}$ to $3322 \text{ gm}^{-2} \pm 626.82$ (Figure 2). The highest root
312 production was in March 2015, 180 days after the experimental setup. In terms of root
313 category, fine and coarse root production also varied significantly between the months of
314 collection ($p < 0.001$). The highest fine root production was in March 2015, and lowest
315 in December 2014. Maximum coarse root growth was recorded in December 2015, 15
316 months after cores were set up and ranged from $598 \pm 85.75 \text{ gm}^{-2}$ to $2785 \pm 468.9 \text{ gm}^{-2}$.
317 In general, fine roots were the main contributor (78% on average) of total root production.

318 A steep decline in root production was seen in June and September 2015. These are the
319 driest months with minimal rainfall. In fact, there was no record for coarse root production
320 in September 2015. Root production increased again in December 2015 but decreased
321 slightly in February 2016. The average root productivity is $12.7 \text{ t ha}^{-1}\text{year}^{-1}$.



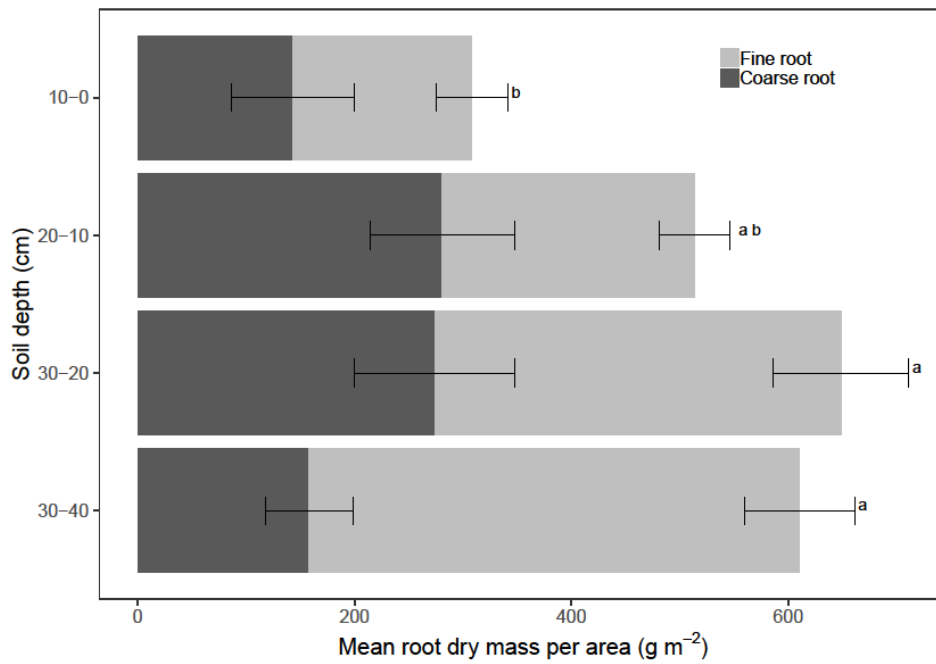
322

323 Figure 2. Root biomass from ingrowth cores retrieved at three-month intervals used to
 324 derive root production (mean \pm SE). Standing root biomass was sampled in February
 325 2016. Bars sharing the same letters indicate no significant difference among total root
 326 biomass ($p < 0.05$).

327 Root depth

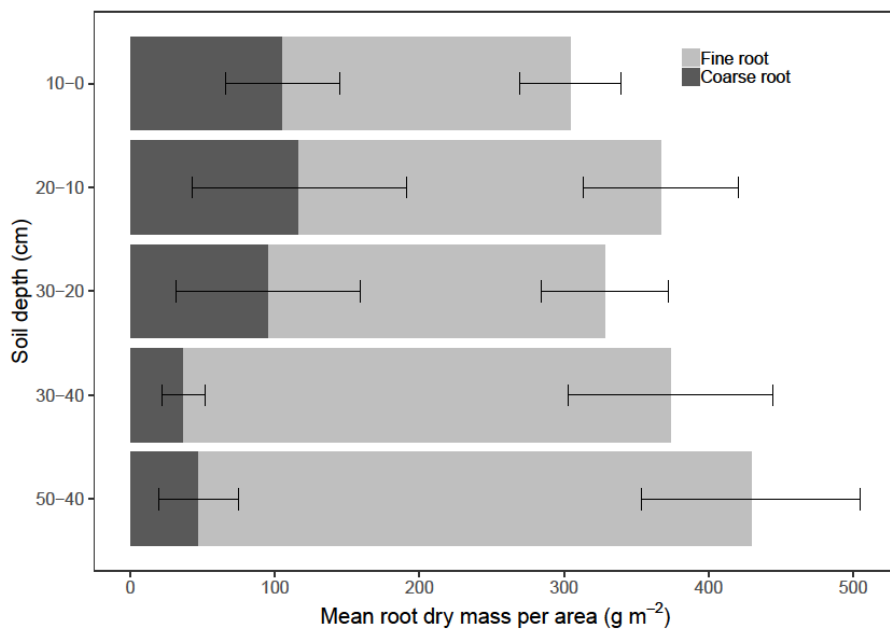
328 Total root stock varied significantly with soil depth ($p < 0.015$). Most of the roots were
 329 found below 10 cm in the soil profile (Figure 3). Fine root biomass was significantly
 330 higher lower down the soil profile ($p < 0.001$), however, there was no significant
 331 difference in coarse root biomass between soil layers. 61% of total root biomass was
 332 found in the 20 to 40 cm horizon.

333 Root production (total roots, fine roots and coarse roots) did not vary significantly with
 334 soil depth (Figure 4). In terms of composition of roots in each soil layer, fine root biomass
 335 increased with increasing depth and represented 78 % of total root production. In contrast,
 336 coarse root production showed a decreasing trend with increasing soil depth.



337

338 Fig 3. Standing root biomass (root stock) according to soil depth. Bars sharing the same
 339 letters indicate no significant difference among soil depth ($p < 0.05$). Mean \pm SE



340

341 Fig 4. Total root production according to soil depth, over the course of 17 months. Mean
 342 \pm SE.

343 Aboveground standing stock and production rate

344 The initial and final aboveground biomasses were 269.73 t ha⁻¹ and 276.54 t ha⁻¹
 345 respectively, thus providing an aboveground production increment of 4.8 t ha⁻¹year⁻¹.

346

347 Above and belowground allocation of biomass and production

348 The standing stock root to shoot ratio was surprisingly low at 0.075 (Table 3). However,
 349 over the course of 17 months, the ratio of below to above ground production was 2.65,
 350 thereby greatly favouring allocation to roots. Hence, 93% of standing stock was allocated
 351 aboveground and 7% belowground, in comparison with above and below ground
 352 production allocation figures of 27% and 73% respectively (Table 3). Similar work to this
 353 study is reported in Tables 4, 5 and 6.

354

355

356 Table 3. Summary of above and belowground parameters.

Above and below ground parameter	Standing stock	Production
Aboveground	277 (t ha ⁻¹)	4.8 (t ha ⁻¹ yr ⁻¹)
Belowground	20.81 (t ha ⁻¹)	12.7 (t ha ⁻¹ yr ⁻¹)
Fine root biomass	12.25 (t ha ⁻¹) (59%)	9.88 (t ha ⁻¹ yr ⁻¹) (78%)
Coarse root biomass	8.56 (t ha ⁻¹) (41%)	2.81 (t ha ⁻¹ yr ⁻¹) (22%)
Based on soil horizon	39.5% total roots in the 0-20 cm soil horizon. 60.5% total roots in the 20-40 cm soil horizon.	55.4% total roots in the 0-30 cm soil horizon. 44.6% total roots in the 30-50 cm soil horizon.

Total root turnover	0.61 (yr ⁻¹)	
Fine root turnover	0.81 (yr ⁻¹)	
Coarse root turnover	0.33 (yr ⁻¹)	
Root:shoot	0.075	2.65
Aboveground allocation	93%	27%
Belowground allocation	7%	73%

357

359 Table 4. Comparison of belowground production in mangrove forest of different regions

Forest type/ setting	Dominant species	Below ground biomass (t ha ⁻¹)	Below Ground production (t ha ⁻¹ yr ⁻¹)	Country	Reference
Island	<i>Sonneratia</i>	38.5	-	Halmahera Island, Indonesia	Komiyama et al. (1988)
Fringe	<i>Rhizophora</i>		2.65	Rotatan Island, Honduras	Cahoon et al.(2003)
Basin	<i>Avicennia</i>		3.02	Rotatan Island, Honduras	Cahoon et al.(2003)
Fringe	<i>R. mangle</i>		3.52	Florida, US	Sanchez (2005)
Basin	<i>Rhizophora</i> , <i>Avicennia germinans</i> and <i>Laguncularia</i>		3.14	Florida, US	Sanchez (2005)
Basin	<i>Avicennia germinans</i>		3.78	Florida, US	Sanchez (2005)
Scrub	<i>R. mangle</i> <i>R. apiculata</i> , <i>A.alba</i> , <i>Xylocarpus granatum</i>	-	3.07 11.02	Florida, US Eastern Thailand	Sanchez (2005) Komiyama (2006)

Basin	<i>Rhizophora and Avicennia</i>	5.25	Twins cays, Belize	McKee et al. (2007a)
Fringe	<i>Rhizophora</i>	3.94	Twins cays, Belize	McKee et al. (2007a)
Transition	<i>Rhizophora</i>	0.82	Twins cays, Belize	McKee et al. (2007a)
	<i>Sonneratia</i>	75	Gazi Bay, Kenya	Tamooch et al. (2008)
Riverine	<i>R. mangle, Laguncularia racemosa and Ceriops erectus</i>	4.65	Shark River, Florida	Castaneda-Moya et al. (2011)
Riverine	<i>Rhizophora, Laguncularia and Aegiceras</i>	6.43	Shark River, Florida	Castaneda-Moya et al. (2011)
Riverine	<i>Rhizophora, laguncularia, Aegiceras</i>	4.69	Shark River, Florida	Castaneda-Moya et al. (2011)
Scrub	<i>Rhizophora</i>	5.61	Taylor River, Florida	Castaneda-Moya et al. (2011)
Scrub	<i>Rhizophora</i>	4.07	Taylor River, Florida	Castaneda-Moya et al. (2011)
Fringe	<i>Rhizophora and Ceriops</i>	4.85	Taylor River, Florida	Castaneda-Moya et al. (2011)

Basin/ landward	<i>Avicennia marina</i>	6.03	3.66	Gazi Bay, Kenya	Lang'at (2013)
Scrub	<i>Ceriops tagal</i>	0.64	0.65	Gazi Bay, Kenya	Lang'at (2013)
Basin/ interior	<i>Rhizophora mucronata</i>		2.54	Gazi Bay, Kenya	Lang'at (2013)
Fringe	<i>Sonneratia alba</i>	5.16	5.16	Gazi Bay, Kenya	Lang'at (2013)
		9.47-30.40	0.46-1.85	Celestun lagoon, Mexico	Adame et al. (2014)
Yela River, soil fertility gradient	Mixed mangroves	4.48-26.41	4.6-11.9	Micronesia	Cormier et al. (2015)
	<i>Avicennia alba</i>	68.4	3.40	Trat River, Thailand	Paungparn et al. (2016)
		2.43-18.69	5.7-28.4	Dongzhai Bay, China	Xiong et al. (2017)
Oligohaline zone	<i>Heritiera fomes</i>	82.3	-	Sundarbans, Bangladesh	Kamaruzzaman et al. (2018)
Oligohaline zone	Mixed mangroves	84.2	-	Sundarbans, Bangladesh	Kamaruzzaman et al. (2018)

Delta	<i>Avicennia alba</i>	20.81	12.7	Kelantan delta, Eastern Malaysian Peninsular	This study (2017)
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362 Table 5. Comparison of aboveground production in mangrove forest of different regions

Forest type/setting	Dominant species	Tree height (m)	Aboveground biomass (t ha ⁻¹)	Aboveground production (t ha ⁻¹ year ⁻¹)	Country	Reference
	<i>Rhizophora apiculata</i>	-	500	6.7	Malaysia	Putz and Chan (1986)
	<i>Rhizophora</i>	3.5	240	6.77	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	<i>Rhizophora and Avicennia</i>	3.5	172	5.62	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	<i>Rhizophora</i>	3.5		4.33	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	<i>Avicennia</i>	3.5	193	1.40	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	<i>Rhizophora apiculata</i>	21.0		12.38	Malaysia	Ong <i>et al.</i> (1995)

Basin/landward	<i>Avicennia marina</i>	5.1	14.5	4.69	Kenya	Lang'at (2013)
Scrub	<i>Ceriops tagal</i>	2.4	11.8	1.97	Kenya	Lang'at (2013)
Basin/interior	<i>Rhizophora mucronata</i>	5.4	125.7	11.73	Kenya	Lang'at (2013)
Fringe	<i>Sonneratia alba</i>	6.1	112.9	5.93	Kenya	Lang'at (2013)
	<i>Avicennia alba</i>	11.3	169.9	8.1	Thailand	Paungparn <i>et al.</i> (2016)
Oligohaline	<i>Heritiera fomes</i>	8.9	153.7	-	Bangladesh	Kamaruzzaman et al (2018)
Oligohaline	Mixed mangroves	-	154.8	17.2	Bangladesh	Kamarazzaman et al (2017)
Delta	<i>Avicennia alba</i>	14.13	277	4.8	Eastern Malaysian Peninsular	This study (2017)

364 Table 6. Comparison of root:shoot ratio in mangrove forest of different regions

Study site	Species	Root:shoot for biomass	Root:shoot for production	References
Indonesia	<i>Sonneratia</i>	0.23		Komiyama et al. (1988)
	<i>Bruguiera</i>	0.29-0.44		
	<i>Rhizophora</i>	0.53-0.67		
Japan	<i>Bruguiera</i>	1.38		Komiyama et al. (1989)
	<i>Rhizophora</i>	1.39		
Thailand	<i>Ceriops tagal</i>	1.05		Komiyama et al. (1989)
Greenhouse	<i>Rhizophora mangle</i>	0.38		Pezeshki et al. (1990)
	<i>Avicennia germinans</i>	0.42		
Queensland	<i>Avicennia marina</i>	0.58		Mackey (1993)
Malaysia	<i>Rhizophora apiculata</i>	0.05		Ong et al. (1995)
Greenhouse	<i>Rhizophora mangle</i>	0.1		McKee (1995b)
	<i>Laguncularia racemosa</i>	0.4-1.5		

	<i>Avicennia germinans</i>	0.2-0.5	
Australia	<i>Avicennia marina</i>	4.1	Saintilan (1997a)
	<i>Avicennia corniculatum</i>	1.9	
Queensland	<i>Avicennia marina</i>	0.4-3.1	Saintilan (1997b)
	<i>Avicennia corniculatum</i>	0.4-1.4	
	<i>Rhizophora stylosa</i>	1.2-1.7	
Japan	<i>Rhizophora stylosa</i>	0.44	Matsui (1998)
Australia	<i>Rhizophora</i>	0.42	
	<i>Ceriops</i>	0.42	
Dominican Republic	<i>Rhizophora mangle</i>		Sherman et al. (2003)
	<i>Laguncularia racemosa</i>	< 0.5	
	<i>Avicennia germinans</i>		
Florida/Greenhouse	<i>Avicennia germinans</i>	> 0.5-1	Sanchez (2005)

	<i>Rhizophora mangle</i>	> 0.5-1	
Shark River, Florida	<i>Rhizophora mangle</i> , <i>Laguncularia racemosa</i> and <i>Ceriops erectus</i>		Castaneda-Moya et al. (2011)
Shark River, Florida	<i>Rhizophora</i> , <i>Laguncularia</i> and <i>Aegiceras</i>		Castaneda-Moya et al. (2011)
Shark River, Florida	<i>Rhizophora</i> , <i>laguncularia</i> , <i>Aegiceras</i>		Castaneda-Moya et al. (2011)
Taylor River, Florida	<i>Rhizophora</i>		Castaneda-Moya et al. (2011)
Taylor River, Florida	<i>Rhizophora</i>		Castaneda-Moya et al. (2011)
Taylor River, Florida	<i>Rhizophora</i> and <i>Ceriops</i>	0.2-1.1	Castaneda-Moya et al. (2011) Lang'at (2012)
Gazi Bay, Kenya	<i>Avicennia marina</i>	3.66	Lang'at (2013)
Gazi Bay, Kenya	<i>Ceriops tagal</i>	0.65	Lang'at (2013)
Gazi Bay, Kenya	<i>Rhizophora mucronata</i>	2.54	Lang'at (2013)
Gazi Bay, Kenya	<i>Sonneratia alba</i>	5.16	Lang'at (2013)

Yela, Kosrae Micronesia		0.074		Cormier et al. (2015)
Kelantan delta, Malaysian Peninsular	<i>Avicennia alba</i>	0.075	2.65	This study (2017)

365

366 Discussion

367

368 Root stock, production and turnover

369 This study showed very high rates of root production and turnover, coupled with
370 relatively low standing stocks with an unusual depth distribution. Estimated annual root
371 production was $12.7 \text{ t ha}^{-1}\text{year}^{-1}$, the second highest rate reported from a mangrove forest.
372 Most other estimates of root productivity are much lower, typically ranging from 2-6 t
373 $\text{ha}^{-1}\text{year}^{-1}$ (Table 4.), although another study in Eastern Thailand produced a similar figure
374 of $11.02 \text{ t ha}^{-1}\text{year}^{-1}$ (Komiyama et al. 2006). The highest reported productivity is 28.4 t
375 $\text{ha}^{-1}\text{year}^{-1}$, from a *Ceriops tagal* stand in China (Xiong et al., 2017). This very high
376 estimate was made by summing a series of cores, rather than by using the in-growth
377 method as employed here and in most other studies. Hence this large difference may be
378 explained by methodological discrepancies. There was also a high estimated total root
379 turnover of 0.61 yr^{-1} , with fine roots turning over more than twice as quickly as coarse
380 roots (0.81 yr^{-1} in comparison with 0.31 yr^{-1}) (Table 3). This rate of fine root turnover
381 exceeds most other estimates, such as those reported from Florida (0.6 yr^{-1} ; Castaneda-
382 Moya et al. 2011), Mexico (0.4 yr^{-1} ; Adame et al., 2014) and Micronesia (0.05 yr^{-1} ;
383 Cormier et al., 2015). The exception is Xiong et al. (2017) who report rates of up to 5.96,
384 driven by their exceptionally high estimates of production; hence again methodological
385 differences may explain this. The current work was also unusual in finding that roots were
386 more abundant lower down the soil profile. A more typical pattern is described by
387 Castaneda-Moya et al. (2011), who observed that root biomass decreased with soil depth
388 in a Florida mangrove forest. This might be explained by the higher concentration of soil
389 nutrient near the soil surface (Castaneda-Moya et al. 2011).

390 Explanations for these unusual findings of large productivity, fast turnover rate and
391 abundant deeper roots may lie in the environmental setting of the Kelantan Delta forest.
392 This is a physically sheltered site with high levels of soil oxygen and low salinity and
393 copious freshwater input, which shows a highly seasonal pattern. Investment in roots for
394 structural strength, for example to resist wave buffeting in very muddy soils, is not
395 necessary here. The high salinity conditions known to encourage high root:shoot ratios in
396 *Avicennia* species elsewhere also do not apply here. The very high productivity and
397 turnover rates of fine roots may be driven by seasonal growth to obtain nutrients such as
398 nitrogen and phosphorus. Rapid root production occurred following the installation of the
399 ingrowth cores in September 2014, peaking in March 2015 and with a secondary peak in

December 2015, coinciding with the monsoon season. This suggests a strong seasonal pattern in root production on the east coast of the Malaysian peninsular. In this region, the northeast monsoon brings heavy rainfall, usually from November to March every year. Paungparn et al. (2016) also reported high mangrove root production after the rainy season in Thailand. Terrestrial forests may show a similar pattern, for example belowground production of the rubber tree (*Hevea brasiliensis*) exhibited seasonal root production which was highly correlated with rainfall (Maeght et al. 2015). Heavy rainfall reduces the salinity of porewater in mangrove systems which favours root growth and stimulates high root production (Cormier et al. 2015). The mean salinity in this study was only 12.08 ± 1.07 ppt, providing ideal conditions for optimum mangrove production.

It is possible that estimated root production and turnover are inflated by experimental artefacts. Cutting all roots before returning them to the ingrowth cores may have provided unnaturally high levels of nutrients, stimulating root growth (McKee 2001). However, the alternative of removing all dead roots would have risked the opposite artefact of underestimated production, and any boost to growth should be quite limited in duration. Xiong et al. (2017) argue that in-growth core methods usually underestimate productivity since they leave inadequate time for a return to steady state conditions. This seems unlikely here given that root biomass exceeded ambient stocks after six months. Subsequent months saw a reduction in biomass, indicating rapid root turnover. Turnover rates calculated across the whole experiment, for total, fine and coarse root biomass, were 0.61, 0.81 and 0.33 respectively (Table 3.). Root turnover rates in this study decreased with increasing root size, as also found by Castaneda-Moya et al. (2011) in a Florida mangrove forest.

In this study, fine roots were the main component of total root stock, providing 59% of the standing root biomass. In terms of root productivity, fine roots accounted for 78% of total root production. This figure is similar to the 62-75% found in Honduran mangroves (Cahoon et al. 2003). This has been explained by the primary role of fine roots in water and soil nutrient acquisition (Sanchez 2005) particularly during early root growth. However, in contrast in Florida and Mexico Castaneda-Moya et al. (2011) and Adame et al. (2014) found a higher fraction of total root biomass was represented by coarse roots. Lower coarse root biomass was found in this study, reflecting very rapid root turnover in this mangrove system, with fine roots making a major contribution to the belowground components.

434 The root standing stock found in this study (20.81 t ha^{-1}) was amongst the lowest reported
435 from the literature for mature forests (Table 4). This may be due to the positioning of the
436 cores relatively far away from the tree trunks, which may have led to an underestimation,
437 particularly of coarse root biomass. Further studies of root biomass should pay attention
438 to this issue. Because of the high aboveground biomass in this study (277 t ha^{-1}) the
439 resulting root:shoot ratio is unusually low.

440

441 Aboveground biomass and production

442 Aboveground biomass measured in the present study is high (277 t ha^{-1}), but comparable
443 with results from other studies (Table 5.). The average stem diameter was $17 \pm 1.0 \text{ cm}$
444 which represents a young stand. A study conducted 30 years ago on a more mature stand
445 in the Malaysian peninsular found aboveground biomass to be twice as high (500 t ha^{-1}
446 and a mean DBH of 50 cm) as in the present study (Putz and Chan 1986). Aboveground
447 biomass of mature mangrove forests is generally greater at lower latitudes, which can be
448 explained by the variation in temperature (Komiyama et al. 2008).

449 Annual aboveground production of *Avicennia alba* in this study ($4.8 \text{ t ha}^{-1} \text{ year}^{-1}$) is
450 similar to that of *Avicennia marina* in Kenya ($4.69 \text{ t ha}^{-1} \text{ year}^{-1}$) (Lang'at 2013), but lower
451 than aboveground production of the same species in Thailand ($8.0 \text{ t ha}^{-1} \text{ year}^{-1}$)
452 (Paungparn et al. 2015). Other aboveground studies in a mangrove forest in Sri Lanka
453 also showed low production ($1.40 \text{ t ha}^{-1} \text{ year}^{-1}$) (Amarasinghe and Balasubramaniam
454 1992) as compared with this study (Table 4).

455

456 Correlation between environmental data and roots data

457 Root production did not significantly correlate with any of the measured soil nutrient
458 concentrations or any of the physiochemical parameters, although there was a trend
459 towards increased root growth with increased soil nitrogen. Previous studies have shown
460 that root production in mangroves might be more dependent on the available phosphorus
461 (P), for example in the Floridian mangroves, (Castaneda-Moya et al. 2011; Adame et al.
462 2014; Poret et al. 2015). However, root production shows contrasting responses to soil P
463 in other studies, as it has been found to increase with soil P in Celestun Lagoon, Mexico
464 (Adame et al. 2014), while it increases with P deficiency within the Everglades (Florida,
465 USA) (Castaneda-Moya et al. 2011).

Salinity is often an important environmental factor determining root production. The maximum root production recorded here during the monsoon season in March (2015) and December (2015) is likely to be because of reductions in salinity. This finding is similar to the study of Thai mangroves which also had high root production during the monsoon season (Paungporn, 2016), and conforms with the finding of Xiong et al. (2017) that fine root production is higher in less saline areas.

Biomass allocation to above and belowground production

Mangroves growing on soil with poor nutrient content allocate most of their resources to grow belowground biomass as a strategy to optimize limited resources (Castaneda-Moya et al 2013). In this study, the root:shoot ratio for standing stock was 0.075, similar to that measured by Cormier et al. (2015) in the mangroves of Micronesia (Table 6). Root:shoot ratio values from the present study and that of Cormier et al. (2015) are much lower than those of 0.4 to 4.1 reported from other mangrove forests (Saintilan a and b 1997) (Table 6.). These results reflect higher biomass investment aboveground in a productive deltaic mangrove forest and are consistent with the higher allocation of biomass aboveground also observed in a productive riverine mangrove forest (Castaneda-Moya et al. 2013).

The root:shoot productivity ratio was 2.65, much higher than the ratio found for standing stocks (0.075). This high productivity and turn-over of roots probably reflects the good environmental conditions at the study site, with relatively high levels of dissolved oxygen and low salinity in the soil porewater, which stimulate root production. Xiong et al. (2017) also reported highest rates of fine root production and turnover in sites with high nutrients and low salinity.

Conclusion

In this study, a productive riverine mangrove forest allocated a large proportion of total standing biomass to the above ground components, particularly in the tree stems. In contrast, belowground productivity was higher than aboveground, and was one of the highest yet recorded in a mangrove forest, with the difference between high estimated root productivity and low standing stock implying rapid root turnover. The benign conditions at the field site, with low salinity and little wave impact, may explain this unusually high root productivity and turnover.

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